PATTERNS OF GEOGRAPHIC DISTRIBUTION AND THEIR IMPLICATIONS ON THE PHYLOGENY OF PUYA (BROMELIACEAE)

G. S. Varadarajan[1]

Puya (± 185 species) is widespread at altitudes from sea level to 5000 m and has an extensive range of distribution from Costa Rica to Chile. Previous studies of this genus have been almost entirely taxonomic in nature due to the paucity of field collections and field data. Using extensive field and herbarium data, the present work investigates *Puya* phylogeny based on geographic distributions and cladistic relationships within the genus. Ten geographical regions in the Andean Cordilleras and one region on the Chilean coast constitute centers of diversity where species of *Puya* are concentrated. Allopatric, endemic, or relatively narrow distributions in mountain ranges or valleys suggest that most species were allopatrically derived. Disjunct distributions are evident in a number of allied species and have resulted from vicariance and long-distance dispersal. Several lineages appear to have radiated both vertically (especially in the central Andes) and horizontally (in the northern Andes) during the Pliocene and Pleistocene when climatic and vegetational pulsations were frequent occurrences. A phylogenetic model presented here for *Puya* describes species divergence from the Guayana Highlands to the northern Andes and via the central Andes to Chile. This model emphasizes that while arid cycles generally favored speciation, some episodes in conjunction with uplift of tectonic units caused extinction of lineages.

Puya Molina (± 185 species) is the second largest genus of subfamily Pitcairnioideae of the Bromeliaceae (Varadarajan, 1988). It is widely distributed from Costa Rica to Chile, especially in the Andean Cordilleras. A very small number of species extend eastward into the Guayana Highlands (Guayana) and Amazonian Brazil. Only three other bromeliad genera—*Aechmea* Ruiz & Pavon, *Pitcairnia* L'Hérit., and *Tillandsia* L.—are more widely distributed than *Puya* (L. B. Smith & Downs, 1974, 1977, 1979). Growth forms of *Puya* range from small tuberous herbs to massive palmlike plants (Figure 1). Habitats of different species are diverse, occurring from sea level to nearly 5000 m (Varadarajan, 1986, 1988, 1989a; Varadarajan & Gilmartin, 1987).

It has been shown that analysis of geographic distributions often provides interesting insights that aid in discerning the phylogeny of a group (e.g., Humphries, 1981; Platnick, 1981). Despite the extensive distribution of *Puya*, research has not progressed much beyond the level of basic taxonomy (L. B. Smith & Downs, 1974). This situation is due to the paucity of field collections

---

[1]Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138, U. S. A. Current Address: School of Agriculture, Tuskegee University, Tuskegee, Alabama 36088, U. S. A.

FIGURE 1.   Diversity of growth forms of *Puya*: a, *P. raimondii,* a remarkable species with a gigantic habit. This flowering individual is nearly 30 feet tall. A massive trunk, formidable spiny foliage, and a columnar inflorescence make it a very conspicuous plant amidst the treeless, rocky habitats of Bolivia. b, *P. trianae,* a small to medium sized (< 1 m) species, presently known from various paramo habitats of Venezuela, Colombia, and Ecuador. c, *P. chilensis,* a species with sympatric populations widespread in several arid localities of Chile. d, *P. brittoniana,* a species attaining 50–60 cm in height; previously

and field data. The complexity within *Puya* is evident from a few recent studies (e.g., Varadarajan, 1987a, 1987b, 1988, 1989a; Varadarajan & Brown, 1988; Varadarajan & Gilmartin, 1988a, 1988b). These studies also emphasize the importance of data from biogeography, pollination studies, ecology, and eco-physiology for elucidating evolutionary phenomena. The principal objectives of this work are to investigate the geographic distributions of various species and examine their inferences on the phylogeny of *Puya*.

METHODS AND OBSERVATIONS

FIELD AND HERBARIUM RESEARCH

Field work for this study has been conducted in Argentina, Bolivia, Chile, Colombia, Ecuador, and Venezuela. The data collected (Varadarajan, 1987a, 1987b, 1988, 1989a) include three major components: descriptive details of the 57 species of *Puya* collected (e.g., growth habit, caudex and foliage type, indumentum morphology, inflorescence morphology, petal color, mode of cap-sule dehiscence, and estimates of seed number; local distributions of species within their habitats and geographic range (Varadarajan, unpubl. MS); and descriptions of the new species encountered (Varadarajan, 1989b; Varadarajan & Flores, 1990). Field collections consist of plant parts preserved in liquid fixatives and voucher specimens deposited in a number of herbaria (TABLE 1).

Herbarium collections of 140 species of *Puya* from 25 major herbaria in South America and the United States have also been studied. In many instances my field collections have supplemented the original author's observations and subsequent herbarium data (Varadarajan, 1988, 1989a). Herbarium and field studies were useful for determining precise habitat types, clarifying the tax-onomy of some problematical species, estimating overall geographic and/or altitudinal range of species, and understanding the interrelations between habitats and phenology and their phylogenetic implications.

Habitats

Most species of *Puya* are specific to particular habitat types that range from semixeric to extremely xeric. At high elevations dry mountain slopes, rock outcrops, open grassy and boggy meadows, cloud forests, and paramos include semixeric to moderately xeric habitats. At low elevations savannas and thorn woodlands contain some semixeric habitats. Habitats associated with monte, sierras, punas, and coastal desert vegetation are extremely xeric. A compre-hensive account of the habitats of *Puya* is in preparation (Varadarajan, MS).

Phenology

Phenology was studied in selected species of *Puya* and included recognition of distinct stages of morphological change in plants from seed germination

known only from the type collection, this taxon is sparsely distributed in the punas of Bolivia. A total of only three populations of this species has been encountered by the author during his explorations. (All photographs by the author.)

TABLE 1. Field collections of Puya made by Varadarajan and associates.[1]

TAXA	COLLECTION NUMBERS	COUNTRY OF COLLECTION (KNOWN DIVERSITY CENTER)	DISTRIBUTIONAL SUBCLASS
P. aequatorialis André var. *aequatorialis* André	1423, 1426, 1430	Ecuador (IV, V)	1b
P. aequatorialis André var. *albiflora* André	1418	Ecuador (IV, V)	1a
P. aristeguietae L. B. Smith	1188	Venezuela (II)	1c
P. assurgens L. B. Smith[2]	1257	Argentina (X)	1a
P. atra L. B. Smith[2]	1446, 1453	Bolivia (IX)	1a
P. berteroniana Mez	1480, 1482, 1486, 1490, 1492	Chile (XI)	2c
P. brittoniana Baker[2]	1466	Bolivia (VIII)	1a
P. cardenasii L. B. Smith[2]	1442, 1463	Bolivia (IX)	2a
P. castellanosii L. B. Smith[2]	1476	Argentina (X)	1a
P. chilensis Molina	1484, 1488	Chile (XI)	2c
P. clava-herculis Mez & Sodiro	1435, 1436	Ecuador (IV, V)	2b
P. coerulea Lindley var. *coerulea*	1491	Chile (XI)	2b
P. coerulea Lindley var. *intermedia* (Smith & Looser) Smith & Looser	1493	Chile (XI)	2b
P. compacta L. B. Smith[2]	1438	Ecuador (V)	1a
P. ctenorhyncha L. B. Smith[2]	1469	Bolivia (VIII)	1a
P. dyckioides (Baker) Mez var. *dyckioides*	1256, 1475	Bolivia, Argentina (IX, X)	1b
P. dyckioides (Baker) Mez var. *novare* Varadarajan[3]	1477	Argentina (X)	1a
P. ferruginea (Ruíz & Pavón) L. B. Smith	1272, 1278, 1295, 1311, 1448, 1467	Bolivia (VI–IX)	1d
P. floccosa (Linden) E. Morren ex Mez	1170, 1172, 1174, 1175, 1185	Venezuela (I–III)	1d
P. fosteriana L. B. Smith[2]	1464	Bolivia (VIII)	1a
P. gilmartinii Varadarajan & Flores[3]	1481	Chile (XI)	2a
P. glabrescens L. B. Smith	1299, 1300, 1303, 1305, 1307, 1309, 1449	Bolivia (IX)	1c

TABLE 1. Continued

Taxa	Collection Numbers	Country of Collection (Known Diversity Center)	Distributional Subclass
P. glomerifera Mez & Sodiro[2]	1417	Ecuador (IV, V)	1c
P. hamata L. B. Smith	1422	Ecuador (IV–VI)	2b
P. harmsii (Castellanos) Castellanos[2]	1245	Argentina (X)	1b
P herzogii Wittmack	1301, 1302, 1304	Bolivia (IX)	2a
P. humilis Mez[2]	1298, 1444, 1450, 1451	Bolivia (IX)	2a
P. lanata (HBK.) Schultes[2]	1424	Ecuador (V)	1b
P. leptostachya L. B. Smith[2]	1445	Bolivia (VIII, IX)	1b
P. lilloi Castellanos	1229, 1235, 1264, 1236, 1474	Argentina (X)	1b
P. maculata L. B. Smith[2]	1434	Ecuador (V)	1a
P. meziana Wittmack[2]	1273	Bolivia (VIII)	1b
P. mirabilis (Mez) L. B. Smith	1223, 1226, 1230, 1233, 1237, 1263	Argentina (IX, X)	1d
P. mollis Baker ex Mez[2]	1470	Bolivia (VI–VIII)	1d
P. nana Wittmack[2]	1461	Bolivia (IX)	1a
P. nutans L. B. Smith[2]	1429, 1432	Ecuador (V)	2a
P. pearcei (Baker) Mez[2]	1286, 1291, 1447, 1472	Bolivia (VIII, IX)	1b
P. pygmaea L. B. Smith[2]	1428, 1437	Ecuador (V)	2a
P. raimondii Harms	1465	Bolivia (VII–IX)	1b
P. retrorsa Gilmartin[2]	1419, 1420, 1440, 1441	Ecuador (between IV & V)	1b
P. riparia L. B. Smith	1274, 1275, 1276	Bolivia (VIII)	1a
P. sanctae-crucis (Baker) L. B. Smith var. *sanctae-crucis*	1454, 1457, 1458	Bolivia (VIII, IX)	1b

TABLE 1. **Continued**

TAXA	COLLECTION NUMBERS	COUNTRY OF COLLECTION (KNOWN DIVERSITY CENTER)	DISTRIBUTIONAL SUBCLASS
P. sanctae-crucis (Baker) L. B. Smith var. *verdensis* Varadarajan[3]	1459	Bolivia (IX)	1a
P. smithii Castellanos	1479	Argentina (X)	1b
P. sodiroana Mez[2]	1427, 1431	Ecuador (V)	2a
P. solomonii Varadarajan[3]	1471	Bolivia (VIII)	1b
P. spathacea (Grisebach) Mez	1240, 1243, 1268	Argentina (outside of X, XI)	1b
P. stenothyrsa (Baker) Mez	1310, 1312, 1468	Bolivia (VIII)	1b
P. trianae Baker[2]	1189, 1439	Venezuela, Ecuador (II, III, V)	1d
P. tristis L. B. Smith[2]	1306, 1308	Bolivia (IX)	2a
P. tuberosa Mez[2]	1455	Bolivia (IX)	1a
P. tunarensis Mez[2]	1296, 1452	Bolivia (IX)	2b
P. ultima L. B. Smith[2]	1277	Bolivia (VIII)	1a
P. ushae Varadarajan[3]	1460	Bolivia (IX)	1a
P. venusta Philippi	1483, 1487	Chile (XI)	2b
P. yakespala Castellanos[2]	1478	Argentina (X)	1a
P. zakiana Varadarajan[3]	1425	Ecuador (V)	1a

[1] Voucher specimens housed in one or more of the following herbaria: GH, LAP, LPB, MO, NY, PORT, SALT, SEL, US, VEN, WS; for details of diversity centers and distribution classes see text.

[2] Taxa previously known from five specimens or fewer.

[3] New taxa encountered.

TABLE 2.   **Most commonly observed patterns of phenology in polycarpic species of Puya.**[1]

PHENOLOGICAL CHARACTERISTICS RECORDED	PATTERNS OF SEASONAL PHENOLOGICAL CHANGES	
	SPECIES IN LOWER LATITUDES[2]	SPECIES IN SOUTHERN LATITUDES[3]
Seed germination and vegetative growth	Completed in 1–5 years	Completed in 1–5 years
Initiation of scape	February	September
Differentiation of inflorescence		
Initiation of flowers		
Differentiation of flowers		
Anthesis		
Pollination	September	February
Fruit set	October	March
Seed development		
Capsule maturation and dehiscence		
Seed dispersal	January	August

[1] Nonseasonal phenological changes are irregular, not synchronized with seasons; some years are characterized by much longer periods of vegetative growth and others by greatly extended periods of flowering and fruiting (examples: *Puya pearcei, P. stenothyrsa*). Successive (complex) phenological changes occur in sympatric groups where the changes are not synchronized with yearly seasons (examples: *Puya clava-herculis, P. nutans,* and *P. pygmaea*).

[2] Example: *Puya retrosa.*

[3] Example: *Puya spathacea.*

through seed dispersal (TABLE 2). There appears to be an interesting correlation between phenology and geographic distribution, especially in the following contexts: (a) sympatric species groups; (b) overlapping species distributions within the same geographical range; and (c) occasional sympatric distribution of predominantly isolated species.

Species of *Puya* are perennial, and with a few exceptions all are polycarpic. Phenology of monocarpic species is well illustrated by *P. raimondii* (FIGURE 1). This gigantic species continues to grow vegetatively for seven to ten years. The transition from a vegetative to the reproductive phase appears to be somewhat abrupt, and the flowering period lasts for up to three years. The nearly twelve-foot tall, indeterminate inflorescence tends to grow rather rapidly after it attains three to four feet in height. The final phase of inflorescence growth, however, appears to be gradual. Although seeds are abundantly produced (about 400 seeds estimated per capsule), the germination rate is extremely low (< 1%). The seed remains dormant for nearly two years.

Polycarpic species exhibit at least three distinct phenological patterns (TABLE 2). In some species (e.g., *Puya spathacea* and *P. mirabilis*) phenological cycles synchronize with yearly seasonal changes. While the phenological pattern is nonseasonal in some widespread species (e.g., *P. ferruginea*), it is complex in others. The following group of co-occurring species in Ecuador illustrates one complex pattern. Within the assemblage of *P. clava-herculis, P. nutans,* and *P.*

pygmaea, P. pygmaea begins its early reproductive phase (inflorescence differentiation) when *P. clava-herculis* enters the final reproductive phase (fruit and seed setting), but *P. nutans* remains in a vegetative phase.

ANALYTICAL RESEARCH

Results of the analysis of herbarium and field data are presented in the following section, and some are summarized on the MAP and in FIGURES 2–4. Phylogenetic interpretations of *Puya* are founded on the individual species distributions, species subsets, their putative cladistic relationships, and similar data known for organisms occurring in the same region.

Geographic Distributions

The principal objective in analyzing the distributions of *Puya* was to recognize specific geographic regions where multiple species are concentrated. This was done by mapping the sites of occurrence of every species. Regions that contain five to forty species are circumscribed here as centers of diversity (see MAP). The area of each diversity center ranges approximately from 12,000–25,000 km².

Cladistic Analysis

A series of procedural steps were involved in the cladistic analysis of various species of *Puya*. The first step was to delimit tentative monophyletic subsets or groups of species and analyze these subsets together in order to reconstruct the phylogeny of the genus. In addition to species subsets, several isolated taxa that did not associate with other individuals or species groups became evident. These isolated taxa displayed only autapomorphies. Monophyletic species subsets recognized here by synapomorphies are of two categories: (1) allied pairs of species that occupy putative terminal branches within a larger (somewhat unresolved) cladogram, and (2) alliances of three to several species that constitute a principal lineage.

Three principal sources aided in my initial choice of species subsets for the analysis. First, the diagnostic key to species of Smith and Downs (1974) suggested a number of pairs or groups of taxa that share multiple characters. Several of these polythetic groups were tested (Sanders, 1981; Wiley, 1981) and were found to be monophyletic (e.g., *Puya* subgenus *Puya*). Second, my continued observations of various developmental stages of species in the field, supplemented by herbarium studies, provided a better definition of some morphological traits (e.g., inflorescence, indumentum). This approach allowed me to recognize additional monophyletic species subsets (e.g., the *Puya tuberosa* complex). Third, a re-examination of several previously neglected, unusual characters (e.g., lustrous bracts, caudex) suggested a few more monophyletic species assemblages.

Data bases with usually less than ten characters were prepared for the subsets of *Puya*. The ancestral and derived states of these characters were determined
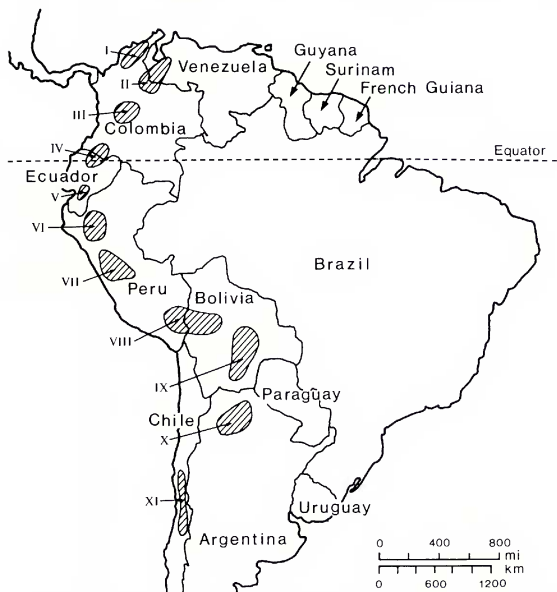
MAP. Geographic locations of centers of diversity of *Puya*. The approximate latitudinal and longitudinal limits of each center are given in parentheses. For other details see text. I, Sierra Nevada de Santa Marta (10°5'–11°2' N, 73°2'–74°2' W); II, eastern cordillera of Colombia and Mérida Andes (5°8'–8°5' N, 71°6'–73°3' W); III, Cundinamarca (4°–5°5' N, 73°3'–75° W); IV, southwestern Colombia and northern Ecuador (0°–36' N, 76°–78°3' W); V, south-central Ecuador (2°–4° S, 78°5'–79°5' W); VI, northern Peru (6°–8° S, 77°–79°2' W); VII, central Peru (9°2'–12° S, 75°–77°2' W); VIII, Titicaca (13°6'–17° S, 67°5'–72° W); IX, southern Bolivia (16°5'–21°5' S, 63°3'–66°7' W); X, northwestern Argentina (22°3'–28° S, 64°–67°8' W); XI, Chile (26°–36°5' S, 69°–72°8' W).

by the outgroup method (Stevens, 1980; Watrous & Wheeler, 1981). Cladograms were manually constructed in accordance with the procedures discussed by Sanders (1981). Provisional outgroup for the species of *Puya* subgenus *Puya* could be any species of the putative sister taxon, *Puya* subgenus *Puyopsis*. Morphological and/or distributional criteria provided the basis for the choice of outgroups for the other species subsets recognized.

RESULTS

Results of the distributional data and of the cladistic analysis address three important questions. Which geographic regions are characterized by relatively high concentration of species? What patterns do these distributions underlie? What is the correlation between geographic distributions and suggested cladistic affinities of species? Each question is discussed below.

CENTERS OF DIVERSITY

All the geographic regions that constitute the following eleven centers of diversity of *Puya* are in South America (see MAP). Center I (Sierra Nevada de Santa Marta) is the most northern and isolated unit of the Andes in Magdalena region in northern Colombia. Center II (eastern cordillera of Colombia and Mérida Andes) covers the northeastern section of Colombia between Norte de Santander and Boyaca, and neighboring Venezuela including Táchira, Mérida, and Trujillo regions. Center III (Cundinamarca) consists of the central part of the eastern cordillera of Colombia. Center IV (southwestern Colombia and Northern Ecuador) includes the territory approximately between the area where the three Andean Cordilleras are divided (Valle del Cauca, Nariño in Colombia) and the volcanic sites of Imbabura in northern Ecuador. Center V (south-central Ecuador) extends between the Cañar and Zamora regions. Center VI (northern Peru) encompasses part of the lowlands of the Amazonas and San Martín regions and the Cordillera Oriental of the Peruvian Andes in the Cajamarca and La Libertad regions. Center VII (central Peru) lies between the Ancash and Ayacucho regions, mainly along the Cordillera Oriental. Center VIII (Titicaca) includes the Cordillera Oriental and Altiplano. It stretches across Lake Titicaca between the Apurimac-Arequipa regions in Peru and the La Paz region in Bolivia. Center IX (southern Bolivia) consists of the eastern part of the Altiplano and the adjoining Cordillera Oriental covering the Cochabamba, Chuquisaca, Potosi, and Tarija regions. Center X (northwestern Argentina) covers the Salta and Jujuy regions. Center XI (Chile) extends between the Antofagasta in the north to Bío Bío in the south.

Center I contains the lowest number of species (five), while centers VII, VIII, and IX harbor the highest species number (nearly forty). All but center XI encompass extensive altitudes (800–5000 m), while center XI includes a much smaller range (sea level to approximately 2000 m). Each center is separated from the closest adjacent one by a distance of at least 200 km. Nearly 75% of the species of *Puya* occur within one or more of the diversity centers circumscribed here, and some species occupy two to three adjacent centers (e.g., *P. clava-herculis, P. dyckioides,* and *P. hamata*) as well as occurring in the intervening areas (e.g., *P. ferruginea.*) Rarely, a few species occur only in the interdiversity regions (e.g., *P. retrorsa* and *P. spathacea*).

DISTRIBUTION PATTERNS

Geographical distributions of species of *Puya* are allopatric and sympatric (TABLE 3).

TABLE 3. **Key characteristics of the distributional classes of Puya.**

DISTRIBUTION CLASS AND SUBCLASS	STANDS	NO. OF INDIVIDUALS PER STAND (AVERAGE)	OCCURRENCE WITHIN DIVERSITY CENTER(S)	EXAMPLES
1. Allopatric				
a. Locally endemic	Usually single	<15	Confined to 1 center	*P. castellanosii*
b. Locally widespread	Multiple	20–30	1 or more centers	*P. lilloi*
c. Predominantly allopatric, widespread, occasionally sympatric	Multiple allopatric and single sympatric	<15	Typically in 1 center; sometimes 2 adjacent centers	*P. glabrescens*
d. Allopatric with extensive distributions	Multiple	30–50	Always in more than 1 center	*P. floccosa*
2. Sympatric				
a. Locally endemic, sympatric	Single	<15	Confined to 1 center	*P. nutans, P. pygmaea,* & *P. sodiroana*
b. Nonendemic, sympatric	Multiple	15–30	1 or more centers	*P. bicolor, P. goudotiana,* & *P. lineata*
c. Nonendemic, replicate sympatric	Multiple	Variable	1 center	*P. berteroniana, P. chilensis, P. gilmartinii,* & *P. venusta*

Allopatric Distributions

Allopatric distributions are characterized by conspecific populations or population systems in diverse, geographically widely separated habitat types. Nearly two-thirds of the species of *Puya* are allopatric on mountain slopes and in valleys, and about one-half are narrow (local) endemics. The range and pattern of species distribution within diversity centers serve as secondary criteria for recognizing subclasses of allopatry.

1a. ALLOPATRIC, LOCAL ENDEMICS (TABLE 3). Allopatric species that are also local endemics occupy relatively few stands but are known from all diversity centers. Distributional territories of these allopatric species are usually restricted to peripheral parts of a diversity center where other species are notably absent. *Puya brittoniana* (FIGURE 1), *P. castellanosii,* and *P. yakespala* illustrate these typical features. The first species comprises a total of three population systems within a radius of about 25 km in the punas of western Bolivia (center VIII). The three known populations of *P. castellanosii* are native to the Cachi, Molinos, and Brealito sites at about 3000 m elevation in the Calchaquíes valleys in northwestern Argentina (center X), while *Puya yakespala* is known only from a single population system in the Yakespala puna slopes of northwestern Argentina at about 4000 m elevation (center X).

1b. ALLOPATRIC, LOCALLY WIDESPREAD (TABLE 3). Allopatric species may be locally widespread in one or two diversity centers. *Puya pearcei*—a good example of a species with multiple stands—is known from cloud forests and cloud forest-puna transitional zones in centers VIII (La Paz region) and IX (Chapare region). *Puya spathacea,* native to north-central Argentina, also conforms to the typical features of this subclass. However, its distribution pattern appears to be somewhat peculiar since the territory of this species is situated several hundreds of kilometers outside of centers X and XI, where other species of *Puya* are not known to exist. *Puya raimondii* (FIGURE 1) is yet another example of this subclass. This allopatric species consists of disjunct multiple stands in centers VIII and IX, which are separated from one another by great distances.

1c. WIDESPREAD, PREDOMINANTLY ALLOPATRIC, AND OCCASIONALLY SYMPATRIC (TABLE 3). When allopatric species consist of multiple stands, some stands may be sympatric with other species within a single diversity center. Species of this subclass (e.g., *Puya glabrescens,* center XI) include fewer individuals per stand in sympatric sites than in allopatric sites. Allopatric sites are found at midelevations among low montane forests, while sympatric sites are in the subalpine to alpine vegetations at higher elevations. Species native to sympatric sites are narrow endemics. *Puya glabrescens* has allopatric populations in scrub forests (2000–2500 m); it is sympatric with *P. herzogii* (Mount Tunari region), *P. humilis* and/or *P. tunarensis* (Pojo region) in various puna habitats (3500–4000 m).

1d. ALLOPATRIC WITH EXTENSIVE DISTRIBUTIONS (TABLE 3). Very few allopatric species (e.g., *Puya floccosa, P. ferruginea,* and *P. mirabilis*) are widespread in two or more diversity centers. Notable characteristics of these species are large

population size (with at least 50 individual plants per population) and extensive intra-population variability. In terms of territory and altitude, the distribution of *P. floccosa* is unmatched by any other member of the genus. This species extends from Costa Rica to Colombia in the Andes (centers I–III), and eastward into the Venezuelan/Brazilian Guianas where its altitudinal range is approximately 3000 m. There are two morphological variants of *P. floccosa*. *Puya ferruginea* is known from southern Ecuador to central Bolivia (centers V–IX). At least two distinct population systems of *P. ferruginea* occur at mid-elevations, each characteristic of cloud forests and highly arid alpine vegetation. *Puya hamata* (centers IV–VI) and *P. mirabilis* (centers IX–X) are also widely distributed in multiple diversity centers.

Sympatric Distributions

Sympatric distributions are characterized by an assemblage of two or more species whose populations or population systems share the same habitat type. About 10–15% of the species of *Puya* appear to be typically sympatric. Spatial distributions of individual species in a common habitat present some variations. Sometimes conspecific populations of sympatric species are intermingled with one another in the same habitat without clear boundaries (e.g., *P. chilensis, P. coerulea,* and *P. venusta* in center XI). By contrast, some sympatric groups (e.g., *P. aristeguietae* and *P. trianae,* in center II) occur only in isolated stands within a habitat. The extent of distributions of the individual taxa and some putative cladistic relationships within the members of the sympatric group provide variations for recognizing subclasses in this category.

2a. LOCALLY ENDEMIC SYMPATRIC SPECIES (TABLE 3). Endemic sympatric species of this subclass are characterized by narrow distributional ranges. Each species may have few to several isolated stands. Individual plants of a stand are sparsely spaced within the habitat. *Puya compacta, P. nutans, P. pygmaea,* and *P. sodiroana* are sympatric and locally endemic to a few paramos of Ecuador (center V, Azuay Province). The habitats of *P. compacta* and *P. sodiroana* are dry slopes whereas those of the other species are swampy meadows.

2b. NON-ENDEMIC SYMPATRIC SPECIES (TABLE 3). Typically, species of this subclass occur in one or two contiguous centers in various sympatric combinations. For instance, *Puya bicolor* Mez, *P. goudotiana* Mez, *P. lineata* Mez, and *P. trianae* (FIGURE 1) are sympatric in a paramo site in center III. However, in other areas of center III, *P. bicolor, P. cleefii* L. B. Smith & Read, and *P. santosii* Cuatrecasas are sympatric. *Puya goudotiana* is sympatric with either *P. killipii* Cuatrecasas or *P. santanderensis* Cuatrecasas in center II. *Puya lineata, P. nitida* Mez, and *P. santosii* are sympatric in various sites of center III. *Puya trianae*—perhaps the most widespread among the sympatric species—is sympatric with *P. aristeguietae* and *P. cardonae* L. B. Smith in center II, and *P. clava-herculis* and *P. pygmaea* in center V.

2c. NON-ENDEMIC, REPLICATE SYMPATRIC SPECIES GROUPS (TABLE 3). A group of fairly widespread species may be found together repeatedly in several sites. One species group in Chile illustrates this subclass. *Puya alpestris* Poeppig, *P.*
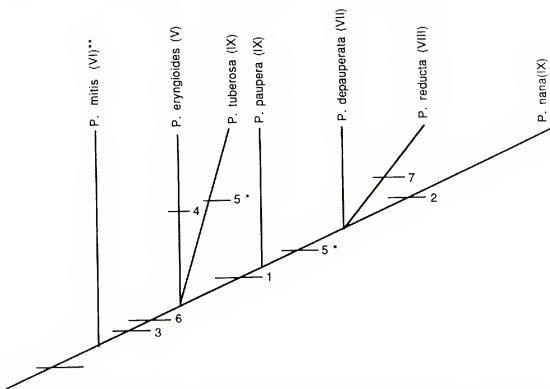
FIGURE 2.   Cladogram of the *Puya tuberosa* complex. The outgroup (*P. mitis* Mez) and the ingroup share an apomorphy (dwarf growth habit) against *P. wurdackii* (plants 1 m tall or taller). Roman numerals indicate diversity centers, arabic numerals signify apomorphies of characters; single asterisks indicate homoplasies and double asterisks, outgroups. Data matrix and characters for taxa included are presented in TABLE 4.

berteroniana, P. boliviensis Baker, *P. gilmartinii,* and *P. chilensis* (FIGURE 1) occur in various combinations and are encountered in several localities (see below). *Puya berteroniana* and *P. chilensis* are the most frequent species in any sympatric assemblage. Similar replicate sympatric groups appear to be rare in *Puya.*

CLADISTIC ANALYSIS AND DISTRIBUTIONS

The results of cladistic analysis may be examined from a distributional perspective of the various members of a monophyletic group. Conversely, the distributional data may also be described from a cladistic perspective of sympatric groups.

The *Puya tuberosa* complex (FIGURE 2; TABLE 4) illustrates a monophyletic group in which the individual sister taxa are allopatric and geographically separated by great distances. This subset of *Puya* is found in several diversity centers, although the individual species are locally endemic to particular centers (subclass 1a). Sister species of this subset as well as other groups are geographically disjunct by distances of a few to several hundred kilometers (TABLE 5).

The monophyletic group *Puya* subgenus *Puya* (FIGURE 3; TABLE 6) reveals some interesting distribution pattern types. A part of this group in center XI consists of replicate sympatric species (subclass 2c; e.g., *P. alpestris* and *P.*

TABLE 4.   **Data matrix of Puya tuberosa complex and its outgroup.**

SPECIES	CHARACTERS[1]						
	1	2	3	4	5	6	7
P. mitis	A	A	A	A	A	A	A
P. eryngioides	A	A	B	B	A	B	A
P. depauperata	B	A	B	A	B	B	A
P. paupera	B	A	B	A	A	B	A
P. nana	B	B	B	A	B	B	A
P. reducta	B	A	B	A	B	B	B
P. tuberosa	A	A	B	A	B	B	A

[1] List of characters: 1, underground rhizome/bulb (A) present, (B) absent; 2, scape (A) lax and conspicuous, (B) condensed and short; 3, inflorescence (A) simple, (B) compound; 4, flowers (A) pedicellate, (B) subsessile; 5, floral bracts (A) toothed, (B) entire; 6, flowers (A) nodding, (B) erect; and 7, scape bracts (A) membranous to coriaceous, (B) chartaceous.

chilensis in the Bío Bío region; *P. berteroniana* and *P. chilensis* in the Coquimbo and Valparaiso regions; *P. berteroniana, P. boliviensis, P. chilensis,* and *P. gilmartinii* in the Atacama-Antofagasta regions). *Puya berteroniana* may also be allopatric along the dry slopes of the Andes (ca. 2000 m). *Puya castellanosii* and *P. weddeliana* are allopatric, local endemics (subclass 1a) while the allopatric *P. raimondii* consists of disjunct multiple stands.

Locally endemic sympatric groups and non-replicate assemblages do not include cladistically closely related taxa. Non-replicate sympatric groups differ from site to site. Cladistic analysis of the sympatric group including *Puya bicolor, P. goudotiana,* and *P. lineata* (subclass 2b) indicates affinities for each taxon with allopatric species characterized by narrow distributions and wide geographical disjunctions (FIGURE 4).

TABLE 5.   **Examples of geographically allied disjunct species pairs in Puya.**

| SPECIES	DIVERSITY CENTER(S)
Species disjunct in contiguous centers	
P. aristeguietae and *P. goudotiana*	II & III
P. killipii and *P. nitida*	
P. micrantha and *P. pearcei*	IX & X
P. fosteriana and *P. weberiana*	
P. castellanosii and *P. chilensis*	X & XI
P. coerulea and *P. smithii*	
Species with major disjunctions	
P. floccosa and	I–III
P. spathacea	outside of X & XI
P. nivalis and	I
P. yakespala	X
P. nutans and	V
P. venezuelana	II
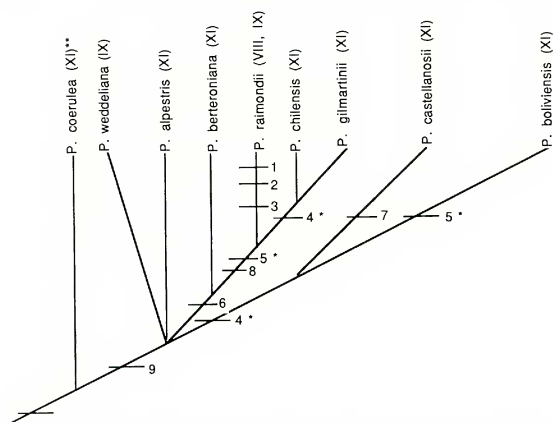
FIGURE 3.   Cladogram of *Puya* subgenus *Puya*. The outgroup (*P. coerulea*) and the ingroup share an apomorphy (spirally twisted postanthesis petals) against *Pitcairnia paniculata* (Ruiz & Pavon) Ruiz & Pavon (straight postanthesis petals). Roman numerals indicate diversity centers, arabic numbers signify apomorphies of characters; single asterisks indicate homoplasies and double asterisks, outgroup. Data matrix and characters for taxa included are presented in TABLE 6.

DISCUSSION

Results of the analyses of geographic distributions and cladistic relationships among species of *Puya* provide insights into the phylogenetic history of divergence lineages and some likely causes and consequences. In addition, these results suggest that a number of species were allopatrically derived. Restricted occurrence and habitat specificity of many species indicate that the isolating mechanisms are geographical. The paraphyletic or polyphyletic nature of most sympatric groups reflects local radiations of several independent phyletic lineages within a geographic center. There is no direct evidence for hybridization of species within the sympatric complexes. Mechanisms that isolate these sympatric species are likely to be genetic.

PHYLOGENETIC HISTORY OF DIVERGENCE OF SPECIES OF PUYA

The literature on the neotropical climatic and vegetational history in conjunction with the geographic distribution of species, habitats, and diversity centers of *Puya* allows for a presentation of a model of phylogenetic divergence of various species lineages. This phylogenetic model emphasizes some likely

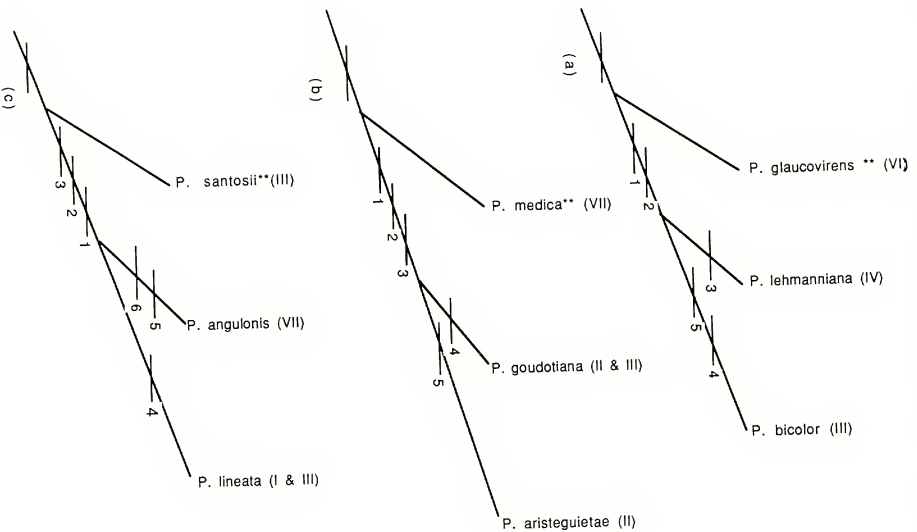TABLE 6. **Data matrix of Puya subgenus Puya and its outgroup.**

SPECIES	CHARACTERS[1]								
	1	2	3	4	5	6	7	8	9
P. coerulea	A	A	A	A	A	A	A	A	A
P. raimondii	B	B	B	A	B	B	A	B	B
P. weddeliana	A	A	A	A	A	A	A	A	B
P. castellanosii	A	A	A	B	?	A	B	A	B
P. chilensis	A	A	A	B	B	B	A	B	B
P. alpestris	A	A	A	A	A	A	A	A	B
P. boliviensis	A	A	A	B	B	A	A	A	B
P. gilmartinii	A	A	A	B	B	B	A	B	B
P. berteroniana	A	A	A	A	A	B	A	A	B

[1] List of characters: 1, caudex (A) noncolumnar, often prostrate, (B) stout and columnar; 2, plants (A) polycarpic, (B) monocarpic; 3, leaf rosette (A) at ground level, (B) above ground level; 4, leaf blades (A) with strongly contrasting surfaces (at least in part), (B) concolorous; 5, petals (A) blue/blue-green, (B) yellow/yellow-green/greenish white; 6, inflorescence branches (A) numbering 30 or less, (B) numbering 80 or more; 7, inflorescence indument (A) nonferruginous, (B) ferruginous; 8, floral bracts (A) distinctly exceeded by sepals, (B) equaling or exceeding sepals; and 9, sterile apex in inflorescence (A) absent, (B) present.

routes of divergence from a previously proposed geographical region of primary differentiation.

Initial Divergence

Diversity centers of *Puya* from I to X are confined to the Andes, and center XI is in Chile (MAP). Characteristic species habitats within these centers indicate that divergence of many lineages occurred principally in paramos (northern Andes), punas (central Andes), and coastal deserts (Chile). We know from recent studies (Varadarajan, 1986; Varadarajan & Gilmartin, 1988a) that the genera of the Pitcairnioideae evolved in the Guayana, and some of them (e.g., *Pitcairnia* and *Puya*) later expanded in the Andes. It is intriguing, however, that species of *Puya* are abundant only in the moderately to extremely xeric habitats of the Andes and not in the semixeric habitats of the Guayana. At least two explanations warrant consideration in this connection. The first explanation contends that only a few species evolved in the Guayana prior to a major proliferation in the Andes. This idea is concurrent with the preponderance of more diverse xeric habitats in the Andes than in the Guayana (Sarmiento, 1975). According to the second explanation, the ancestral lineages of *Puya* in the Guayana were essentially semixeric, occupying such habitats as sandstone bluffs, talus slopes, and igneous "lajas." The moderately xeric lineages in the Andes descended from the semixeric ones and invaded extremely xeric sites at high elevations. This hypothesis also rests on the assumption that several semixeric or moderately xeric lineages became extinct in the Guayana as a result of a series of catastrophic environmental changes (van der Hammen, 1982), some of which were reflected in the frequent contraction and expansion of savannas (Huber, 1982). During comparable time periods, however, the Andean regions experienced more or less equitable environments that were

(a)

P. glaucovirens ** (VI)

1

2

3

5

4

P. lehmanniana (IV)

P. bicolor (III)

(b)

P. medica** (VII)

1

2

3

4

5

P. goudotiana (II & III)

P. aristeguietae (II)

(c)

P. santosii**(III)

3

2

1

6

5

P. angulonis (VII)

4

P. lineata (I & III)

congenial to the survival and proliferation of the descendant lineages (see van der Hammen, 1982, for related discussions).

Colonization and Diversification in the Northern Andes

Two migratory routes may have been important for the radiation of *Puya* from Guayana into the Andes. The first was via the eastern highlands of Colombia into the northern Andes of Colombia and Ecuador (centers II to IV); the second was via the Peruvian Amazon region into the central Andes (centers VI to VIII).

Guayana, an expansive floristic province of South America (Steyermark, 1982), is characterized by its underlying sedimentary mantle (Roraima) that constitutes most of the highlands. The mantle stretches out into eastern Colombia in a series of isolated "mesitas," adjoining the Cordillera Macarena and the flanks of the Andes (Maguire, 1970). The physical contiguity between Guayana and the Andes may have facilitated a direct migration of some Guayanan species of *Puya* into the Colombian Andes (eastern Cordillera, centers II and III).

The distribution of a sizable number of species of *Puya* in the paramos and the adjoining subparamos and montane habitats (elevations 2000 m and above) would be important in the context of divergence. A plausible explanation may be that at lower elevations species initially invaded the montane forest habitats and subparamos, from which they migrated to the paramos at high elevations. These migrations were probably best suited to glacial periods. During glacial times paramo areas were geographically much expanded, and the intervening distances between them were much reduced. This physio-geographic situation, combined with a massive production of wind-dispersed seeds, facilitated extensive colonization by several species. During interglacial periods, on the

---

FIGURE 4. Cladograms of the members of a sympatric species group (*Puya bicolor, P. goudotiana,* and *P. lineata*). a, Alliance of *Puya bicolor.* The outgroup (*P. glaucovirens*) and the pair of sister species share an apomorphy (stout pedicels) against *P. adscendens* L. B. Smith (slender pedicels). Polarity is established in the following characters: 1, dry inflorescence axes: angled to cylindrical; 2, racemes: polystichously flowered to densely flowered toward apex; 3, sepals: symmetric to asymmetric; 4, flowers: erect to downwardly secund; 5, primary bracts: shorter than or equalling sterile bases of racemes to longer than sterile bases of racemes. b, Alliance of *P. goudotiana.* The outgroup (*P. medica*) and the pair of sister species share an apomorphy (petals 4 cm long or longer) against *P. phelpsiae* L. B. Smith (petals 2–5 cm long or smaller). Polarity is established in the following characters: 1, scape bracts and primary bracts: persistent to disintegrating rapidly after anthesis; 2, primary bracts: pectinate-serrate to entire; 3, sepals: carinate to ecarinate; 4, flowers: erect-spreading to recurved; 5, petals: blue-bluish green to white. c, Alliance of *P. lineata.* The outgroup (*P. santosii*) and the pair of sister species share an apomorphy (very densely imbricate scape bracts) against *P. laccata* Mez (lax scape bracts). Polarity is established in the following characters: 1, inflorescence: compound to simple; 2, floral bracts: entire to pectinate-serrate; 3, floral bracts: not lustrous to lustrous; 4, sepals: obtuse to apiculate; 5, sepals: not lustrous to lustrous; 6, pedicels: simple to compound and winged. Roman numerals indicate diversity centers, arabic numbers signify apomorphies of characters; single asterisks indicate homoplasies and double asterisks, outgroups.

contrary, paramos were fragmented into discrete "islands" in which isolation was followed by speciation (for related discussions see Cleef, 1979; Cuatrecasas, 1957, 1979; van der Hammen, 1974, 1979, 1982).

The Sierra Nevada de Santa Marta deserves mention in this discussion. While it constitutes the northernmost and geographically the most ancient structural unit of the Andes (Simpson, 1975), the Sierra Nevada de Santa Marta may not necessarily have been a region of initial invasion by species of *Puya*. This suggestion is based on the contemporary idea of Guayanan differentiation of the genus and on the lack of direct geological and ecological continuity between Guayana and the Sierra Nevada de Santa Marta. These floristic provinces are separated by a region of predominantly mesic communities—the "llanos" and the adjoining mosaics of low vegetation—that historically separated xeric species of some plant families between the Andes and Guayana (see Steyermark, 1982). The latter situation is true for *Puya* as well. This suggests that the Sierra Nevada de Santa Marta may be a refuge area for species of *Puya* where taxa were dispersed from centers II and/or III. Subsequently, they became isolated as a result of unusually long dry periods and unique geological events. Preliminary assessments of phyletic relationships suggest relictual status for the species of *Puya* native to the Sierra Nevada de Santa Marta.

Expansion in the Central Andes

The Amazonian lowlands, including pockets of xeric habitats, have perhaps provided geographical continuity between Guayana and the eastern slopes of the Peruvian and Bolivian Andes. The lineages that initially colonized these low Andean habitats further extended into high elevation punas and adjoining arid regions. A substantial number of lineages seem to have proliferated in the alpine regions of Peru and Bolivia (centers VII and VIII). Present evidence suggests that at least some of these high elevation lineages have descended directly from the lower elevation species (TABLE 7). The process of radiation and differentiation in the central Andes probably occurred at different times during glacial cycles than did similar events in the northern Andes. Specifically, glacial periods in the central Andes saw the development of significant water barriers across the Altiplano as a result of the presence of a massive system of lakes and rivers; these water barriers fragmented habitats and led to population isolation and speciation (Simpson, 1975; Varadarajan, 1986; Varadarajan & Gilmartin, 1988a). In the northern Andes, by contrast, speciation events occurred during interglacial times.

Radiation into Chile

There are at least three central Andean ancestral sources for the species lineages now native to Chile. The present distributional and cladistic analyses of *Puya* subgenus *Puya* (FIGURE 3) suggest that these ancestral taxa (similar to *P. raimondii, P. weddeliana,* and *P. castellanosii*) may have been from centers VIII, IX, or X (MAP). A vicariance model (see below) is conceivable for the differentiation of *Puya* subgenus *Puya* in light of some available evidence (TABLE 4).

TABLE 7. **Examples of high altitude species of Puya and their lower altitude allies.**

HIGH ALTITUDE TAXA			ALLIED LOWER ALTITUDE TAXA			
Species	Altitudinal range (in m)	Vegetational type	Species	Altitudinal range (in m)	Vegetational type	Diversity center
P. harmsii (Castellanos) Castellanos	3000–3600	Monte, punas	*P. lilloi* Castellanos	800–2000	Transitional forests	X
P. dyckioides (Baker) Mez	1300–4000	Scrub, punas	*P. assurgens* L. B. Smith	1800–2000	Low scrub forests	X
P. weberbaueri Mez	2800–4000	Punas	*P. lasiopoda* L. B. Smith	500–2300	Moist forests	VIII

CONVERGENT EVOLUTION IN PUYA

The distribution of habitats (punas, coastal deserts, etc.) within diversity centers suggests evolution of most species of *Puya* under the regime of arid environments. This notion is well attested to by a number of structural (Robinson, 1969; Tomlinson, 1969; Varadarajan, 1986; Varadarajan & Gilmartin, 1987) and physiological (Medina, 1974; Medina *et al.*, 1977; Griffiths, 1984; Griffiths & J. A. C. Smith, 1983; J. A. C. Smith *et al.*, 1986) features. It is important to note that these features are by no means confined to a single phyletic lineage. Climatic history of the Andes (e.g., Simpson, 1975; van der Hammen, 1974) indicates the occurrence of several independent episodes of arid cycles during Pliocene and Pleistocene times when various regions experienced frequent climatic and vegetational pulsations and the uplift of tectonic plates. For example, in the intermountain valleys of the northern Andes xeric environments developed as a result of mountain barriers, which produced rain shadow effects by intercepting the movement of wet air masses (Gilmartin, 1973; Sarmiento, 1975). In coastal areas, however, aridity resulted from persistent strong winds associated with increased ocean currents and coastal upwelling (Simpson, 1975; van der Hammen, 1974, 1982). Thus, it is possible to conclude that different species lineages of *Puya* evolved in response to various, often similar environmental pressures. Similar xeric adaptations displayed by these lineages probably illustrate convergent evolution.

RADIATION OF SPECIES IN RELATION TO ALTITUDE

Expansion of species lineages of *Puya* in the Andes was probably vertical as well as horizontal. The idea of vertical radiation has been postulated for several paramo taxa (Ericaceae, Melastomataceae, Rubiaceae; Chardon, 1938). Modern geographic distributions and phyletic alliances of various lineages of *Puya* suggest that only species confined to the punas (in Peru, Bolivia, and Argentina) could have evolved vertically (TABLE 7). Paramo species of *Puya* generally lack allies at lower elevations. These species radiated by a horizontal mechanism similar to some other paramo-dwelling groups (e.g., *Espeletia, Jamesonia, Diplostephium*; Cuatrecasas, 1957, 1979; A. C. Smith & Koch, 1935; Tryon, 1962).

DISJUNCTIONS

Vicariance and dispersal models explain the origin of disjunctions (Nelson & Platnick, 1981; Platnick & Nelson, 1978; Roe, 1967, 1972; Rosen, 1978; Whalen, 1983). There are apparently various degrees of disjunctions among the species of *Puya* (TABLE 5). Vicariance models postulate the appearance of barriers fragmenting the range of ancestral species. The congruence between the hypothesized cladistic relationships and the area of occurrence of species provides a useful indication of vicariance (see also Croizat *et al.*, 1974; Wiley, 1980, 1981). Such a congruence usually translates into parallel phylogenetic historics involving two or more lineages. Vicariance is a plausible mechanism especially for some high altitude lineages and putatively allied species pairs of *Puya* (TABLE 7). Replicate patterns of occurrences of sympatric groups and allied species pairs also suggest vicariance (TABLE 5).

Dispersal models, on the other hand, portray disjunction in light of dispersal across barriers, which is entirely dependent on unique dispersal abilities within the individual lineages rather than parallel patterns. For instance, the theory of long distance dispersal is compatible with the distribution of the *Puya tuberosa* complex across several intermountain valleys (FIGURE 2). Present evidence indicates that the disjunction of various species in this assemblage is probably an isolated event, not matched by any other subgroups in terms of parallel geographic patterns or cladistic relationships. Major disjunctions also occur as unique patterns in a few independent lineages (TABLE 5). These are undoubtedly an outcome of long distance dispersal.

PHENOLOGY AND GEOGRAPHIC DISTRIBUTION

Distinct phenological trends are correlated with some of the subclasses of geographic distributions of *Puya*. For example, phenological cycles synchronizing with climatic seasons are noted especially in the allopatric taxa (subclasses 1a and 1b). This trend may suggest a relatively long-term local stability of the species. When the range of a species expands over time, it may include environments differing from the parent one(s). This type of distributional change might induce specific (local) modifications in phenological traits. Thus, in species distributed widely across various macroclimates (e.g., species of subclass 1d), the relationship between phenology and the annual seasons is locally altered, revealing no apparent correlations. Phenology in sympatric taxa appears to be complex and remains as yet an intriguing, unexplored subject. To understand this complexity, we need data concerning socio-ecologic relationships, and the evolutionary histories of individual taxa as well as those of the habitats of sympatric species.

SUMMARY AND CONCLUSIONS

A majority of the species of *Puya* are allopatric and narrow endemics. They are most likely allopatrically derived and are isolated by geographic barriers. Speciation in many lineages primarily in the northern and central Andes and Chile resulted from episodes of aridity. Species appear to have colonized high altitudes directly from the differentiation of low elevation lineages as well as by a horizontal mechanism. Allied species became disjunct due to vicariance and dispersal events. Species extinctions probably occurred in a few lineages as a result of the obliteration of habitats brought about by localized arid periods and the uplift of tectonic plates. From Guayana, *Puya* immigrated into the Andes and attained its present range.

ACKNOWLEDGMENTS

LITERATURE CITED

CHARDON, C. E. 1938. Apuntaciones sobre el origen de la vida en los Andes. Bol. Soc. Venez. Ci. Nat. **5**: 1–47.

CLEEF, A. 1979. The phytogeographic position of the Neotropical vascular paramo flora with special reference to the Colombian Cordillera Oriental. Pp. 175–184 *in* K. LARSEN & L. B. HOLM-NIELSEN, eds. Tropical botany. Academic Press, London.

CROIZAT, L., G. J. NELSON, & D. E. ROSEN. 1974. Centers of origin and related concepts. Syst. Zool. **23**: 265–287.

CUATRECASAS, J. 1957. A sketch of the vegetation of the North-Andean province. Proc. VIII Pacific Sci. Congr. **9**: 167–173.

———. 1979. Growth forms of the Espeletiinae and their correlation to vegetation types of the high tropical Andes. Pp. 397–410 *in* K. LARSEN & L. B. HOLM-NIELSEN, eds. Tropical botany. Academic Press, London.

GILMARTIN, A. J. 1973. Transandean distributions of Bromeliaceae in Ecuador. Ecology **54**: 1389–1393.

GRIFFITHS, H. 1984. Ecological distribution of bromcliads in Trinidad and their O ^{13}C values: implications for the use of O values to indicate carboxylation pathways in plants. Pp. 145–174 *in* E. MEDINA, ed. Physiological ecology of CAM plants. International Center for Tropical Ecology (UNESCO-IVIC), Caracas, Venezuela.

——— & J. A. C. SMITH. 1983. Photosynthetic pathways in the Bromeliaceae of Trinidad: relations between life-forms, habitat preference, and the occurrence of CAM. Oecologia **60**: 176–184.

HUBER, O. 1982. Significance of savanna vegetation in the Amazon territory of Venezuela. Pp. 221–244 *in* G. T. PRANCE, ed. Biological diversification in the tropics. Columbia University Press, New York.

HUMPHRIES, C. J. 1981. Biogeographical methods and the southern beeches (Fagaceae: *Nothofagus*). Pp. 177–208 *in* V. A. FUNK & D. A. BROOKS, eds. Advances in cladistics. New York Botanical Garden, Bronx, New York.

MAGUIRE, B. 1970. On the flora of the Guayana Highland. Biotropica **2**: 85–100.

MEDINA, E. 1974. Dark CO$_2$ fixation, habitat preference and evolution within the Bromeliaceae. Evolution **28**: 677–686.

———, M. DELGADO, & J. H. TROUGHTON. 1977. Physiological ecology of CO$_2$ fixation in Bromeliaceae. Flora **166**: 137–152.

NELSON, G. J., & N. I. PLATNICK. 1981. Systematics and biogeography: cladistics and vicariance. Columbia University Press, New York.

PLATNICK, N. I. 1981. Widespread taxa and biogeographic congruence. Pp. 223–236 *in* V. A. FUNK & D. A. BROOKS, eds. Advances in cladistics. New York Botanical Garden, Bronx, New York.

———— & G. J. Nelson. 1978. A method of analysis for historical biogeography. Syst. Zool. 27: 1–16.

Robinson, H. 1969. A monograph on foliar anatomy of the genera *Connellia, Cottendorfia,* and *Navia* (Bromeliaceae). Smithsonian Contr. Bot. 2: 1–41.

Roe, K. E. 1967. A revision of *Solanum* section *Brevantherum* (Solanaceae) in North and Central America. Brittonia 19: 353–373.

————. 1972. A revision of *Solanum* section *Brevantherum* (Solanaceae). *Ibid.* 24: 239–278.

Rosen, D. E. 1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool. 27: 159–188.

Sanders, R. 1981. Cladistic analysis of *Agastache* (Lamiaceae). Pp. 95–114 *in* V. A. Funk & D. R. Brooks, eds. Advances in cladistics. New York Botanical Garden, Bronx, New York.

Sarmiento, G. 1975. The dry plant formations of South America and their floristic connections. J. Biogeography 2: 233–251.

Simpson, B. 1975. Pleistocene changes in the flora of the high tropical Andes. Palaeobiology 1: 273–294.

Smith, A. C., & M. F. Koch. 1935. The genus *Espeletia*: a study in phylogenetic taxonomy. Brittonia 1: 479–543.

Smith, J. A. C., H. Griffiths, & U. Luttge. 1986. Comparative ecophysiology of CAM and C3 bromeliads I. The ecology of the Bromeliaceae in Trinidad. Plant Cell and Env. 9: 359–376.

Smith, L. B., & R. J. Downs. 1974. Pitcairnioideae (Bromeliaceae). Flora Neotropica Monograph 14(1): 1–658. Hafner Press, New York.

———— & ————. 1977. Tillandsioideae (Bromeliaceae). Flora Neotropica Monograph 14(2): 663–1492. Hafner Press, New York.

———— & ————. 1979. Bromelioideae (Bromeliaceae). Flora Neotropica Monograph 14(3): 1493–2142. New York Botanical Garden, Bronx.

Stevens, P. F. 1980. Evolutionary polarity of character states. Ann. Rev. Ecol. Syst. 11: 333–358.

Steyermark, J. 1982. Relationships of some Venezuelan forest refuges with lowland tropical forests. Pp. 189–219 *in* G. T. Prance, ed. Biological diversification in the tropics. Columbia University Press, New York.

Tomlinson, P. B. 1969. Commelinales–Zingiberales iii. Pp. 192–294 *in* C. R. Metcalfe, ed. Anatomy of Monocotyledons. Oxford University Press, London.

Tyron, A. F. 1962. A monograph of the fern genus *Jamesonia*. Contr. Gray Herb. 191: 109–203.

Van der Hammen, T. 1974. The Pleistocene changes of vegetation and climate in tropical South America. J. Biogeography 3: 3–26.

————. 1979. History of flora, vegetation, and climate in the Colombian Cordillera Oriental during the last five million years. Pp. 24–32 *in* K. Larsen & L. B. Holm-Nielsen, eds. Tropical botany. Academic Press, London.

————. 1982. Paleoecology of tropical South America. Pp. 60–66 *in* G. T. Prance, ed. Biological diversification in the tropics. Columbia University Press, New York.

Varadarajan, G. S. 1986. Taxonomy and evolution of the subfamily Pitcairnioideae (Bromeliaceae). Ph. D. dissertation. Microfilms International, Ann Arbor, Michigan.

————. 1987a. Explorations for Pitcairnioideae in South America. Part 1. J. Bromeliad Soc. 37: 16–25.

————. 1987b. Explorations for Pitcairnioideae in South America. Part 2. *Ibid.*: 62–66.

————. 1988. Genus *Puya* Molina: relocation of several rare species and some preliminary remarks on geographic distributions and species divergence. Part 1. *Ibid.* 38: 243–247, 254–256.

————. 1989a. Genus *Puya* Molina: relocation of several rare species and some pre-

liminary remarks on geographic distributions and species divergence. Part 2. *Ibid.* **39:** 3–7.

————. 1989b. Novelties of *Puya* Molina I: a new species from Bolivia. *Ibid.*: 121–123.

———— & G. K. BROWN. 1988. Morphological variation of some floral features of the subfamily Pitcairnioideae (Bromeliaceae) and their role in pollination biology. Bot. Gaz. (Crawfordsville) **149:** 82–91.

———— & A. FLORES. 1990. Novelties of *Puya* Molina II: a new species from Chile. J. Bromeliad Soc. **40:** (in press).

———— & A. J. GILMARTIN. 1987. Foliar scales of the subfamily Pitcairnioideae (Bromeliaceae). Syst. Bot. **12:** 562–571.

———— & ————. 1988a. Phylogenetic relationships of groups of genera within the subfamily Pitcairnioideae (Bromeliaceae). Syst. Bot. **13:** 283–293.

———— & ————. 1988b. Seed morphology of the subfamily Pitcairnioideae (Bromeliaceae) and its systematic implications. Am. J. Bot. **75:** 808–818.

WATROUS, L., & Q. WHEELER. 1981. The outgroup method of phylogeny reconstruction. Syst. Zool. **30:** 1–16.

WHALEN, M. D. 1983. Centers of diversity, sympatry, and historical biogeography in the tropical plant genus *Solanum*. The Biol. **65:** 78–95.

WILEY, E. O. 1980. Phylogenetic systematics and vicariance biogeography. Syst. Bot. **5:** 194–220.

————. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley & Sons, New York.